Predator-Prey Population Dynamics

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Predator-Prey model (Lotka-Volterra system)

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Stochastic model as continuous-time Markov chain

A simple Predator-Prey model

- Populations of X prey molecules and Y predator molecules
- Three possible reactions (events)

$$\begin{array}{lrl} \text{1) Prey reproduction:} & X & \to 2X \\ \text{2) Prey consumption to generate predator:} & X+Y & \to 2Y \\ \text{3) Predator death:} & Y & \to \emptyset \end{array}$$

- Each prey reproduces at rate α
  - $\Rightarrow$ Population of X preys $\Rightarrow \alpha X =$ rate of first reaction
- Prey individual consumed by predator individual on chance encounter
  - $\Rightarrow \beta =$ Rate of encounters between prey and predator individuals
  - $\Rightarrow X$ preys and Y predators $\Rightarrow \beta XY =$ rate of second reaction
- Each predator dies off at rate γ
  - $\Rightarrow$ Population of Y predators $\Rightarrow \gamma Y =$ rate of third reaction

The Lotka-Volterra equations

- Study population dynamics $\Rightarrow X(t)$ and $Y(t)$ as functions of time t
- Conventional approach: model via system of differential eqs.
  - $\Rightarrow$ Lotka-Volterra (LV) system of differential equations
- Change in prey $(dX(t)/dt) =$ Prey generation - Prey consumption
  - $\Rightarrow$ Prey is generated when it reproduces (rate $\alpha X(t)$)
  - $\Rightarrow$ Prey consumed by predators (rate $\beta X(t)Y(t)$)

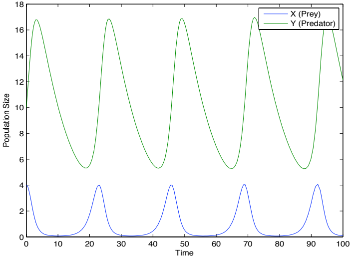
$$\frac{dX(t)}{dt} = \alpha X(t) - \beta X(t)Y(t)$$

- Predator change $(dY(t)/dt) =$ Predator generation - consumption
  - $\Rightarrow$ Predator is generated when it consumes prey (rate $\beta X(t)Y(t)$)
  - $\Rightarrow$ Predator consumed when it dies off (rate $\gamma Y(t)$)

$$\frac{dY(t)}{dt} = \beta X(t)Y(t) - \gamma Y(t)$$

Solution of the Lotka-Volterra equations

- LV equations are non-linear but can be solved numerically

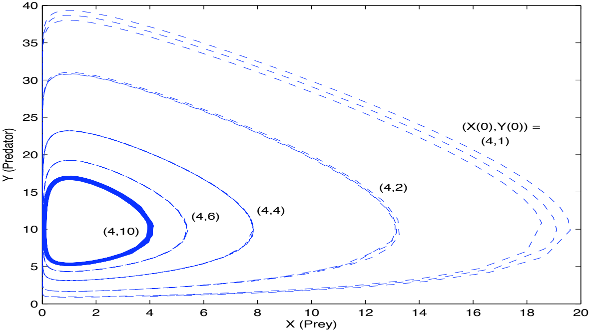


- Prey reproduction rate $\alpha = 1$
- Predator death rate $\gamma = 0.1$
- Predator consumption of prey $\beta = 0.1$
- Initial state $X(0) = 4, \; Y(0) = 10$
- Boom and bust cycles

- Start with prey reproduction $>$ consumption $\Rightarrow$ prey $X(t)$ increases
- Predator production picks up (proportional to $X(t)Y(t)$)
- Predator production $>$ death $\Rightarrow$ predator $Y(t)$ increases
- Eventually prey reproduction $<$ consumption $\Rightarrow$ prey $X(t)$ decreases
- Predator production slows down (proportional to $X(t)Y(t)$)
- Predator production $<$ death $\Rightarrow$ predator $Y(t)$ decreases
- Prey reproduction $>$ consumption (start over)

State-space diagram

- State-space diagram $\Rightarrow$ plot $Y(t)$ versus $X(t)$
  - $\Rightarrow$ Constrained to single orbit given by initial state $(X(0), Y(0))$



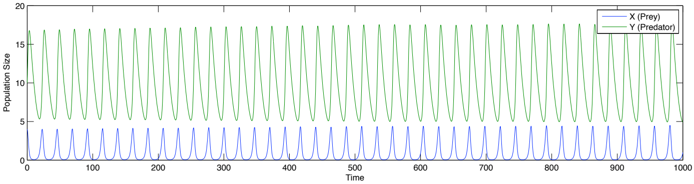
Buildup: Prey increases fast, predator increases slowly (move right and slightly up)

Boom: Predator increases fast depleting prey (move up and left)

Bust: When prey is depleted predator collapses (move down almost straight)

Two observations

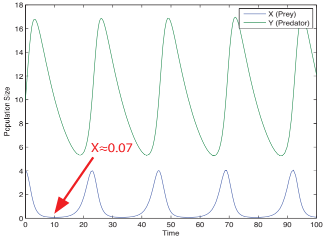
- Too much regularity for a natural system (exact periodicity forever)



- $X(t)$, $Y(t)$ modeled as continuous but actually discrete. Is this a problem?
- If $X(t)$, $Y(t)$ large can interpret as concentrations (molecules/volume)

  $\Rightarrow$ Often accurate (millions of molecules)
- If $X(t)$, $Y(t)$ small does not make sense

  $\Rightarrow$ We had 7/100 prey at some point!
- There is an extinction event we are missing



Things deterministic model explains (or does not)

- Deterministic model is useful $\Rightarrow$ Boom and bust cycles
  - $\Rightarrow$ Important property that the model predicts and explains
- But it does not capture some aspects of the system
  - $\Rightarrow$ Non-discrete population sizes (unrealistic fractional molecules)
  - $\Rightarrow$ No random variation (unrealistic regularity)
- Possibly missing important phenomena $\Rightarrow$ Extinction
- Shortcomings most pronounced when number of molecules is small
  - $\Rightarrow$ Biochemistry at cellular level ($1 \sim 5$ molecules typical)
- Address these shortcomings through a stochastic model

Stochastic model as CTMC

Predator-Prey model (Lotka-Volterra system)

Stochastic model as continuous-time Markov chain

Stochastic model

- Three possible reactions (events) occurring at rates c_1, c_2 and c_3

  1) Prey reproduction: $X \xrightarrow{c_1} 2X$

  2) Prey consumption to generate predator: $X + Y \xrightarrow{c_2} 2Y$

  3) Predator death: $Y \xrightarrow{c_3} \emptyset$

- Denote as $X(t), Y(t)$ the number of molecules by time t
- Can model $X(t), Y(t)$ as continuous time Markov chains (CTMCs)?
- Large population size argument not applicable

  $\Rightarrow$ Interest in systems with small number of molecules/individuals

Stochastic model (continued)

- Consider system with 1 prey molecule x and 1 predator molecule y
- Let $T_2(1,1)$ be the time until x reacts with y
  - $\Rightarrow$ Time until x, y meet, and x and y move randomly around
  - $\Rightarrow$ Reasonable to model $T_2(1,1)$ as memoryless

$$\mathrm{P}\left(T_2(1,1) > s+t \,\middle|\, T_2(1,1) > s\right) = \mathrm{P}\left(T_2(1,1) > t\right)$$

- $T_2(1,1)$ is exponential with parameter (rate) c_2

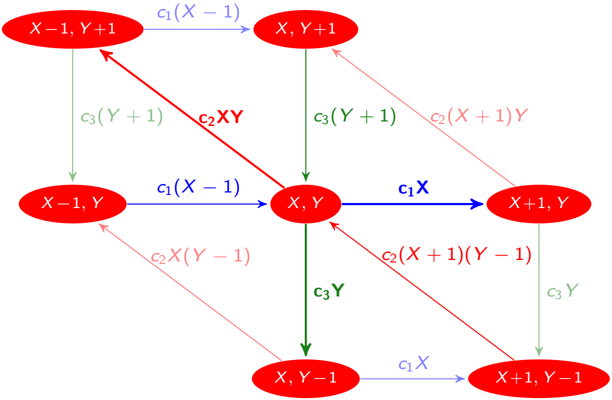
Stochastic model (continued)

- Suppose now there are X preys and Y predators
  $\Rightarrow$ There are XY possible predator-prey reactions
- Let $T_2(X, Y)$ be the time until the first of these reactions occurs
- Min. of exponential RVs is exponential with summed parameters
  $\Rightarrow$ $T_2(X, Y)$ is exponential with parameter c_2XY
- Likewise, time until first reaction of type 1 is $T_1(X) \sim \exp(c_1X)$
- Time until first reaction of type 3 is $T_3(Y) \sim \exp(c_3Y)$

CTMC model

- If reaction times are exponential can model as CTMC

  $\Rightarrow$ CTMC state (X, Y) with nr. of prey and predator molecules

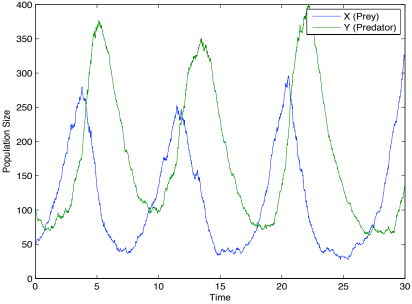


Transition rates

- $(X, Y) \to (X+1, Y)$: Reaction 1 $= c_1X$
- $(X, Y) \to (X-1, Y+1)$: Reaction 2 $= c_2XY$
- $(X, Y) \to (X, Y-1)$: Reaction 3 $= c_3Y$
- State-dependent rates

Simulation of CTMC model

- Use CTMC model to simulate predator-prey dynamics
  - Initial conditions are $X(0) = 50$ preys and $Y(0) = 100$ predators



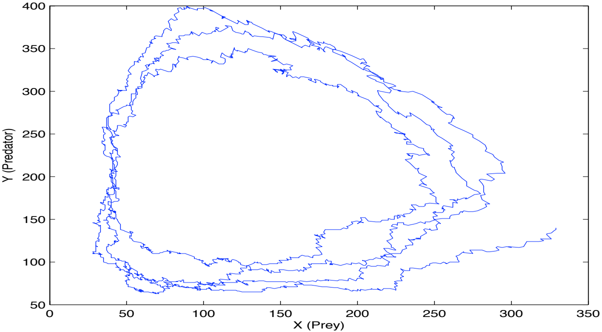
- Prey reproduction rate
  $c_1 = 1$ reactions/second
- Rate of predator consumption of prey
  $c_2 = 0.005$ reactions/second
- Predator death rate
  $c_3 = 0.6$ reactions/second

- Boom and bust cycles still the dominant feature of the system

  $\Rightarrow$ But random fluctuations are apparent

CTMC model in state space

- Plot $Y(t)$ versus $X(t)$ for the CTMC $\Rightarrow$ state-space representation

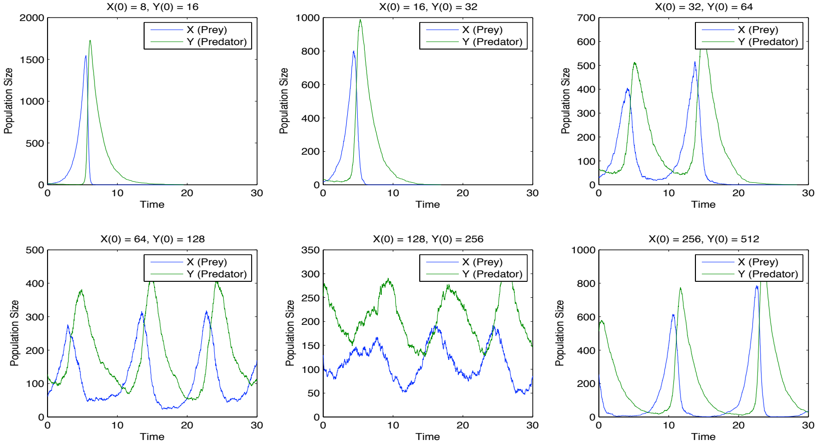


- No single fixed orbit as before

  $\Rightarrow$ Randomly perturbed version of deterministic orbit

Effect of different initial population sizes

- Chance of extinction captured by CTMC model (top plots)



(Notice that Y-axis scales are different)

Conclusions and the road ahead

- Deterministic vs. stochastic (random) modeling
- Deterministic modeling is simpler
  - $\Rightarrow$ Captures dominant features (boom and bust cycles)
- CTMC-based stochastic simulation more complex
  - $\Rightarrow$ Less regularity (all runs are different, state orbit not fixed)
  - $\Rightarrow$ Captures effects missed by deterministic solution (extinction)
- Gillespie's algorithm. Optional reading in class website
  - $\Rightarrow$ CTMC model for every system of reactions is cumbersome
  - $\Rightarrow$ Impossible for hundreds of types and reactions
  - $\Rightarrow$ Q: Simulation for generic system of chemical reactions?